THE BIOLOGY OF ACANTHOSCELIDES ALBOSCUTELLATUS (COLEOPTERA: BRUCHIDAE) ON ITS HOST PLANT, LUDWIGIA ALTERNIFOLIA (L.) (ONAGRACEAE)

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Abstract. – The host range of Acanthoscelides alboscutellatus (Horn) is clarified, and the life history and ecology of A. alboscutellatus on its host plant, Ludwigia alternifolia (L.), is described for populations in the mid-Atlantic region of the U.S. Aspects of the host plant's biology essential to understanding the interaction of this univoltine seed predator with its host are also described. The parasitoids and predators of A. alboscutellatus are documented.

Key Words: Life history, host plant, bruchid parasitoids

The seed beetle. Acanthoscelides alboscutellatus (Horn) (Coleoptera: Bruchidae), is a host-specific seed predator of Ludwigia alternifolia (L.) (Onagraceae) (Hamilton 1892, Bridwell 1935, Bissel 1940, pers. obs.). Despite sustained interest in the systematic and ecological relationships between Acanthoscelides and their host plants (Johnson 1970, 1981a, b, 1983, Center and Johnson 1974, Kingsolver and Johnson 1978) and interest in the evolution of reproductive structures in the genus Ludwigia (Eyde 1977, 1978, 1981, Peng and Tobe 1987, Ramamoorthy and Zardini 1988), little information is available on the life history of A. alboscutellatus or the interaction of A. alboscutellatus and L. alternifolia. The purpose of this paper is to describe the natural and life history of A. alboscutellatus and those features of the biology of its host plant, parasitoids, and predators that contribute toward understanding the interaction of A. alboscutellatus with its host. The observations and timing of events reported here describe populations of *L. alternifolia* and *A. alboscutellatus* in the College Park, Maryland area.

Originally described by Horn (1873), A. alboscutellatus is considered to be a divergent species of Acanthoscelides, and its placement in the genus is uncertain. Johnson (1983) recognized 14 species groups in the genus and tentatively placed A. alboscutellatus in the flavescens group even though the male genitalia differs markedly from other members of this group. Acanthoscelides alboscutellatus is an atypical member of the genus in several respects. Of the approximately 155 species within the genus known to occur in Central and North America, A. alboscutellatus is the only species that uses a member of the plant family Onagraceae as a host (Johnson 1970, 1981a). Moreover, in contrast to many other Acanthoscelides, the larvae of A. alboscutellatus do not feed and develop within a single seed but instead feed on many small seeds and pupate in a cocoon that they construct within the many-seeded fruit capsule of *L. alternifolia*. Finally, *A. alboscutellatus* may be unique among the Bruchidae in that the architecture of the host plant's fruit imposes constraints on the body size of adult beetles capable of escaping from indehiscent fruit at eclosion. As a result, adult *A. alboscutellatus* eclosing within indehiscent fruit are subjected to selection for small body size (Ott 1990, 1991).

HOST PLANT DOCUMENTATION

Hamilton (1892), Bridwell (1935), and Bissell (1940) reported rearing A. alboscutellatus from the fruit of L. alternifolia. Blatchley (1910) reported L. palustris to be the host of A. alboscutellatus based on the occurrence of this plant in an area where a sweep sample yielded A. alboscutellatus. Cushman (1911) cited Blatchley's findings and subsequently both L. alternifolia and L. palustris have been accepted as hosts of A. alboscutellatus (Johnson 1970, 1983). Blatchley (1910), however, did not rear A. alboscutellatus from the fruit of L. palustris, the accepted criterion for establishing host plants for the Bruchidae. No records of A. alboscutellatus having been reared from L. palustris are known to this author. Townsend (1895) reared some beetles from Glycyrrhiza lepidota (Fabaceae) that he identified as A. alboscutellatus. This host record, however, has never been verified and is considered doubtful (Johnson 1983, J. M. Kingsolver, pers. comm.). In the areas of Maryland, Virginia, and North Carolina surveyed by this author, larval, pupal, and adult A. alboscutellatus have been collected from within the fruit of only L. alternifolia from ≈ 40 populations. Until new documentation suggests otherwise, I assert that L. alternifolia is the only verified host plant of A. alboscutellatus.

THE BIOLOGY OF L. ALTERNIFOLIA

Ludwigia alternifolia occurs from southern Canada to Florida and Texas, and extends from the east coast westward to Iowa and Arkansas (Raven and Tai 1979). Within its range, L. alternifolia is patchily distributed and is restricted to moist habitats such as seepage areas, pond margins, marsh edges, beaver dams, and drainage ditches. Local population size is extremely variable. ranging from tens to thousands of plants. Many habitats colonized by L. alternifolia are characterized by rapid plant succession. Within these habitats, the tenure of L. alternifolia appears to be only a few years. For example, in two populations studied by this author the number of mature L. alternifolia plants decreased over four years from several hundred to less than twenty-five plants in each population. In more stable habitats such as semipermanent seepage areas, tenure may be much longer.

Ludwigia alternifolia is a short-lived perennial possessing a shallow root system that produces from one to five stalks each year (mode = 1, n = 69). Ludwigia alternifolia attains adult size in two to three years and mature plants can reach heights of 0.75 to 2 meters. Variation in edaphic conditions results in variation in plant size, morphology, and fruit number among populations and within populations between years (Ott, unpublished data).

Flowering in L. alternifolia begins in late June, peaks about three weeks later, and continues for up to forty-five days. Flowers occur singly along the numerous branches of each stalk. Within an individual plant, flowering and fruit maturation proceed centrifugally up the stalk. Individual plants vary in both the time at which flowering is initiated and the duration of flowering (Ott, unpublished data). Adult A. alboscutellatus of both sexes regularly visit L. alternifolia flowers and consume both nectar and pollen during the first hours following anthesis (Fig. 1). Anthesis occurs two to four hours after sunrise depending on local environmental conditions. Petals are shed and pollinator visitation ceases four to six hours later. Although adult A. alboscutellatus visit L. alternifolia flowers and may effect some pollination, the primary pollinators currently are the introduced honeybee, *Apis mellifera*, native bumblebees, primarily *Bombus pennsylvanicus*, and the carpenter bee, *Xylocopa virginica*. Forty mature *L. alternifolia* plants monitored during 1984 produced an average of 250 ± 124 flowers (range 54 to 744), abscised no flowers, and aborted less than one percent of the subsequent fruit that developed.

The fruit of *L. alternifolia* is a four-sided capsule (3 to 6 mm in width and 4 to 6 mm in depth), which is fitted with a square top (Figs. 2–5, 7, 8). *Ludwigia alternifolia* fruit contain from 194 to 2143 seeds ($\bar{x} = 920$ \pm 34 (SE), n = 122) which are fed on by larval *A. alboscutellatus*. Seed number is linearly related to fruit size and can be predicted from the width (w) of the fruit top (seed number = -2126.9 + 1608.3 w (in mm); R² = 0.89, *P* < 0.0001, n = 122). Individual seeds average 0.03 mg in weight.

Ludwigia alternifolia fruit expand to full size within seven to ten days of flowering. During August and September the walls of the two to three layers of cells immediately beneath the fruit's epidermis thicken and lignify to form a hard woody capsule (Eyde 1978) (Fig. 3) This capsule is further strengthened by median vascular bundles that effectively bond the four sides of the fruit together, forming a completely sealed vessel (Eyde 1981). Fruit remain attached to the plant. Seeds are dispersed primarily through an apical pore, a circular opening formed at maturity in the fruit top by the abscission of the style and deterioration of subjacent tissue (Raven 1963) (Figs. 4, 10). Fruit begin to gradually dehisce (the top and/ or sides separate) during the winter and spring following their production (Fig. 5). Seeds remaining in fruit are dispersed at this time. Some fruit, however, remain indehiscent for up to one year. The percent of fruit remaining indehiscent varies among plants within populations, among populations, and between years within populations (Ott 1990). The ratio of dehiscent to indehiscent

fruit within and between populations is of major significance to the life history of *A*. *alboscutellatus* for two reasons: indehiscent fruit impose constraints on the body size of adult beetles and dehiscence greatly increases beetles' exposure to harsh environmental conditions during winter months (see below, Ott 1990).

Throughout the latter stage of the flowering/fruiting season, leaves are shed, and the above ground portion of the plant lignifies, becoming woody. Beginning in mid to late winter the basal portion of the stalk begins to deteriorate and the stalk may detach from the root system and fall into surrounding vegetation. This feature of the plant's biology in conjunction with variation in fruit dehiscence generates further variation in the range of conditions that are encountered by overwintering *A. alboscutellatus.*

THE BIOLOGY OF A. ALBOSCUTELLATUS

Oviposition. – Eggs of A. alboscutellatus are deposited singly onto the surface of developing L. alternifolia fruit and are held in place by secretions produced by the female (Fig. 2). Eggs remain glued to fruit for up to several months (Fig. 8). As in many other bruchids (Center and Johnson 1974) eggs are not placed randomly on the surface of fruit. Instead, females prefer to deposit eggs along the edges of the capsules' four sides and on the lower side of the fruit, under either of the two bracteoles (Fig. 2). Both the sepals and bracteoles remain attached to fruit throughout maturation. Few eggs are placed on the fruit's more exposed top and the central areas of the sides.

In natural populations, females begin to oviposit about two weeks after the first L. *alternifolia* flowers appear. In the field, oviposition takes place during the mid-morning to early afternoon hours. In the lab, females deposit viable eggs for up to fifty-two days. This period of time closely matches the host plant's flowering and fruiting season. Once oviposition has been initiated, egg deposition onto individual fruit in the field begins as early as one day after petals are shed, peaks between one and two weeks, and may continue at a decreasing rate for up to four weeks (Ott, unpublished data). As a consequence, the developmental stage of eggs on individual fruit and later the developmental stages of maturing *A. alboscutellatus* within a fruit are often highly variable.

The number of *A. alboscutellatus* eggs observed on individual fruit in natural populations may range up to thirty. The maximum number of adults that can mature within an individual fruit is, however, only ten. The cumulative number of eggs on fruit at the end of the oviposition season is a linearly decreasing function of the time at which a given fruit develops during the fruiting phenology. As a result, variation in flowering phenology results in predictable levels of infestation among plants within populations and even within individual plants (Ott, unpublished data).

Variation in both the number and developmental stages of eggs observed on individual fruit results from oviposition from multiple females. Observations of ovipositing females in the field suggest, and laboratory studies confirm, that females spread their daily output of eggs among many fruit. In the laboratory, fifty-nine individually caged females each provided with ten L. alternifolia fruit that were initially devoid of eggs spread their eggs among the available fruit by depositing an average of 2.07 ± 0.87 eggs per fruit in a twenty-four hour period. When confronted with L. alternifolia fruit that vary in age and egg load, females' choice of fruit on which to oviposit is not random: increasing fruit age and the number of eggs present on fruit inhibit further oviposition (Ott, unpublished).

The eggs of A. alboscutellatus are ellipsodial in shape and average $\approx 0.02 \text{ mm}^3$ in volume (range 10.9 to 30.6 μ m³, n = 594), (Fig. 2). For a cohort of thirty-seven female A. alboscutellatus maintained in the laboratory for the entirety of their reproductive careers (Ott 1990) the average volume of individual eggs was positively correlated with female abdomen volume (r = 0.53, P < 0.0007). These females deposited an average of 91.68 \pm 28.17 eggs (range 45 to 153), and the total number of eggs deposited per female was positively correlated with abdomen volume (r = 0.56, P < 0.0001). The daily output of eggs from individual females captured in the field and allowed to oviposit on virgin fruit in the laboratory for a single twenty-four hour period averaged 6.02 ± 3.69 eggs (range 1 to 14, n = 62).

Beetle development. - First-instar larvae develop in seven to nine days at twentythree °C in the laboratory. Larvae emerge through the ventral surface of the egg chorion and bore directly into the fruit through the capsule wall (Fig. 6). Entering young, fleshy fruit requires three to five days at twenty-three °C. When eggs are deposited on fruit that are partially to completely lignified, larvae are unable to penetrate the fruit wall. The egg chorion remains glued to the fruit and fills with plant wall debris and frass produced by the boring larvae (Fig. 8). The bore holes produced by larvae remain as permanent features of the fruit and allow the number of larvae entering each fruit to be determined at the end of the oviposition season (Fig. 8). Infrequently the chorion becomes partially detached from the fruit before larvae begin boring into the fruit. Larvae then wander about the fruit surface and die.

Once inside the fruit, larvae enter and feed within individual developing ovules. When larval size exceeds ovule size, the larvae move among the ovules and consume all or part of the ovules encountered (Fig. 7). Late instar larvae construct a cocoon using mature seeds cemented together (Fig. 9). The presence of cocoons interferes with the dispersal of seed through the fruit's apical pore (pers. obs.). Cocoons are constructed about four weeks after oviposition, and adult beetles are observed within cocoons forty to forty-seven days after oviposition. Hamilton (1892) reported A. alboscutellatus larvae, pupae, and adults in a sample of fruit collected in late October; however, close examination by this author has shown that A. alboscutellatus overwinter only as adults.

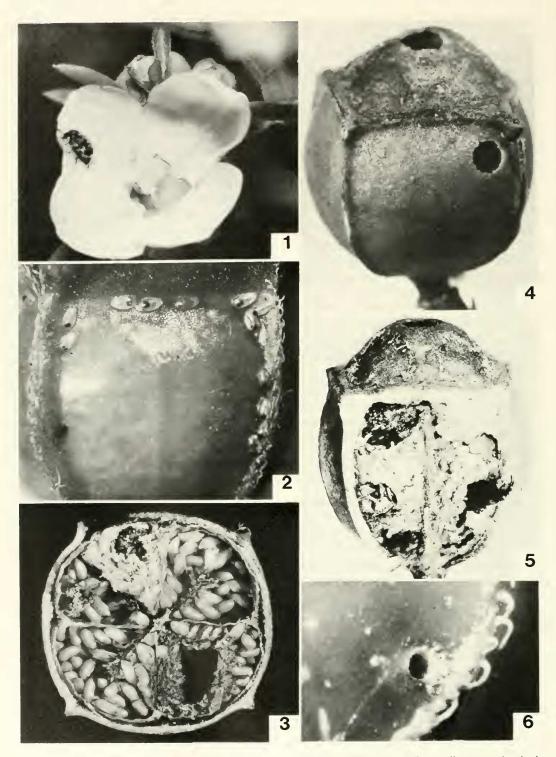
Overwintering.—All adult A. alboscutellatus begin overwintering within cocoons inside indehiscent fruit. The partial to complete dehiscence of fruit, however, exposes overwintering beetles to a variety of overwintering environments. Experimental studies of winter survivorship across the range of conditions created by fruit dehiscence shows that adult A. alboscutellatus have the capability to successfully overwinter in sites other than indehiscent fruit (Ott 1990).

Emergence of adults.-Adult A. alboscutellatus become active beginning with the onset of warm weather as early as mid to late March. Adults eclosing within fruit that have not dehisced do not chew an exit hole through the fruit wall as is typical of many bruchids (Center and Johnson 1974, Johnson 1987). Instead beetles attempt to escape from indehiscent fruit through the fruit's apical pore, which the beetles are capable of enlarging to a limited extent by chewing (Ott 1990) (Fig. 10). Because the diameter of the apical pore is usually less than the beetle's body diameter, beetles eclosing within indehiscent fruit are often trapped within the capsule (Ott 1990) (Fig 10). Beetles may live for up to three months trapped inside fruit but are incapable of reproducing within fruit (see below). Unless the apical pore can be enlarged to permit escape or the fruit dehisces, trapped beetles ultimately die within the fruit.

Colonization of the host plant.—During the one to two month interval between the emergence of beetles from overwintering sites and the initiation of new *L. alternifolia* growth in late April and early May, *A. alboscutellatus* can be found on the vegetation adjacent to dried *L. alternifolia* stalks of the previous year. *Acanthoscelides alboscutel*- *latus* moves onto *L. alternifolia* with the initiation of new plant growth. With the onset of flowering, beetles congregate in pre-flowering buds during the night and can be found on the foliage of *L. alternifolia* at all times.

I have never observed A. alboscutellatus visiting the flowers of any other plant within or surrounding L. alternifolia habitats. This observation, in conjunction with laboratory studies, suggest that adult A. alboscutellatus do not feed on nectar and pollen sources prior to the appearance of L. alternifolia flowers. In the laboratory, populations of A. alboscutellatus housed at ten to twelve °C and supplied daily with water showed no appreciable mortality for up to two months. A period of imaginal diapause, lasting up to several months prior to the appearance of the host plant, appears to be a typical feature of bruchids with univoltine life histories (Biemont and Bonet 1981). Whereas nectar and pollen feeding do not appear to be necessary prior to the flowering of the host plant, association with the host plant appears to be critical to break reproductive diapause in A. alboscutellatus (see below).

Breeding biology. - The mating behavior of A. alboscutellatus is largely unknown. Few copulating pairs have been observed in the field despite extensive observation. Only once was copulation observed among two hundred male-female pairs of previously virgin beetles (beetles extracted from overwintering cocoons) that were housed in the laboratory, supplied with L. alternifolia flowers and fruit, and periodically observed. Yet the females of one hundred and eighty of these pairs produced fertile eggs. Virgin females maintained similarly but isolated from males did not produce eggs. These observations suggest that both the frequency and duration of copulation are low. Studies of females that were collected from natural populations at the onset of the oviposition season and maintained in the laboratory in the absence of males show that, once mated, females are able to produce fertile eggs (\geq



Figs. 1–6. 1, Adult A. alboscutellatus visiting L. alternifolia flower, $10 \times$; 2, A. alboscutellatus eggs developing on the exterior of an immature L. alternifolia fruit, $25 \times$; 3, cross section of a mature (fully lignified) fruit exposing

90% viability) for the duration of their reproductive lifespan (Ott 1990). These results indicate that females store sperm and are not required to mate repeatedly throughout the oviposition season to produce fertile eggs. While females may not mate repeatedly, males are capable of mating with multiple females as shown by the viability of eggs produced by multiple virgin females after mating with a single male.

The reproductive organs of male and female A. alboscutellatus have not been examined during the interval between ecolosion and oviposition, hence the timing of gonadal maturation and mating has not been definitively established. Two studies suggest, however, that female A. alboscutellatus do not receive sperm until the initiation of host plant flowering. In the first study, twenty-five females that eclosed and subsequently became trapped in the presence of at least one male within indehiscent fruit were extracted, separated from the male(s), and housed in the laboratory. Each female was then provided with L. alternifolia fruit and flowers at two day intervals for the duration of the flowering season. These females may have spent up to several weeks trapped with males within indehiscent fruit. None of these females, however, produced fertile eggs suggesting that one or both of the sexes were sexually incompetent during the period following eclosion, and, that while the opportunity may exist, mating does not take place within indehiscent fruit.

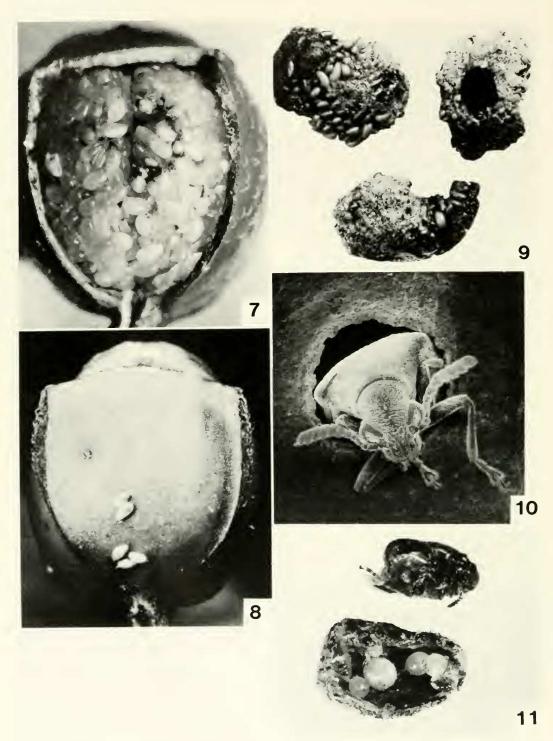
In the second study, twenty-five males and fifty females were collected from a natural population two weeks prior to the initiation of *L. alternifolia* flowering. All twenty-five of the females that were housed in the absence of males but routinely provided with *L. alternifolia* flowers and fruit for the duration of the flowering season failed to produce any eggs, while twenty-two of the twenty-five females treated similarly but housed with males produced fertile eggs. These studies, along with the observation that in natural populations *A. alboscutellatus* eggs first appear on *L. alternifolia* fruit about 12 days after the initiation of flowering, suggest that reproductive competence is acquired at about the time *A. alboscutellatus* begin to feed on the flowers of *L. alternifolia*.

Parasites and predators. - The eggs of A. alboscutellatus are parasitized by Uscana semifumipennis (Girault) (Hymenoptera: Trichogrammatidae). Acanthoscelides alboscutellatus eggs that have been parasitized by U. semifumipennis are readily identifiable because this wasp creates a diagonistic exit hole in the upper surface of the egg chorion at eclosion. Since the egg chorion typically remains attached to the fruit, the number of A. alboscutellatus eggs parasitized by Uscana semifumipennis can be assessed by periodic collection and inspection of L. alternifolia fruit. Uscana semifumipennis undergoes multiple generations of reproduction per season using A. alboscutellatus as a host.

Acanthoscelides alboscutellatus eggs are also preyed upon by the larvae of Adalia bipunctata (Linne) (Coleoptera: Coccinellidae). The larvae of these beetles actively search the surface of L. alternifolia fruit and when A. alboscutellatus eggs are encountered, pierce and consume the contents of the egg chorion. The egg chorion may be detached from the fruit during this process so that the frequency of such predation cannot be assessed as confidently as other mortality sources.

Once inside A. alboscutellatus fruit, L. al-

internal fruit structure, mature seeds and the overwintering cocoons of *A. alboscutellatus*, $20 \times$; 4, mature fruit showing apical pore (top of fruit) and wasp emergence hole (side of fruit), $20 \times$; 5, mature fruit with one side removed (partially dehiscent) showing exposed overwintering cocoons, $20 \times$; 6, *A. alboscutellatus* larval entrance scar in *L. alternifolia* fruit, $50 \times$.



Figs. 7–11. 7, Developing L. alternifolia fruit with one side removed showing larval feeding path and developing seeds, $20 \times$; 8, mature fruit three months after infestation, showing attached egg chorions and larval

ternifolia larvae and pupae are parasitized by five species of chalcid wasps: Dinarmus acutus (Thomson), Zatropis incertus (Ashmead) (Pteromalidae); Eupelmus cyaniceps (Ashmead), Eupelmus brevicauda (Crawford) (Eupelmidae); and Eurytoma sp. (Eurytomidae). Ovipositing wasps first appear during the later half of the flowering/fruiting season. At this time females visit the most mature fruit, which at this time contain lateinstar beetle larvae and pupae. Female wasps insert their ovipositor through the fruit wall and can be observed ovipositing through September and October. All five wasp species have been reared from beetle larvae collected between September and October. Rearing wasp larvae extracted from fruit samples collected during January and February shows that at least two species, Dinarmus acutus and Eupelmus cyaniceps, overwinter as larvae within A. alboscutellatus cocoons. The overwintering hosts of the remaining species, as well as the identities of antecedent host(s) used by these wasps, are unknown. For all five species only one wasp emerges from a single A. alboscutellatus larvae. (The extent of hyper-parasitism is presently unknown.) After eclosion, these parasitoids exit the L. alternifolia fruit by chewing through the lignified fruit wall. This diagonistic scar allows fruit in which beetles have been parasitized to be readily identified (Fig. 4).

Throughout late summer and early fall, coincident with fruit maturation and the opening of the fruit's apical pore, the parasitic mite, *Pyemotes tritici* (Lagrece-Fossat) (Pyemotidae), moves into *L. alternifolia* fruit through the apical pore. Within the fruit, these mites feed and reproduce on all life stages of *A. alboscutellatus* and on the larvae and pupae of parasitic wasps. *Pyemotes tritici* kill their prey; however, not

all beetles and wasps within a mite-infested fruit are necessarily attacked. *Acanthoscelides alboscutellatus* and chalcid wasps killed by *P. tirtici* are identifiable by the exoskeletal remains of the founding female mites (Fig. 11). *Pyemotes tritici* multiply at a prolific rate (up to five hundred nymphs have been collected from the founding females associated with a single beetle larvae). Nymphs move out of infected fruit to colonize adjacent fruit and plants. Mite infection is a major source of mortality for developing and overwintering beetles (pers. obs.).

The fruit of L. alternifolia and their associated fauna are subject to predation by a diversity of vertebrates. During the early fall, White-footed mice, Peromyscus leucopus, and field voles, Microtus pennsylvanicus, selectively eat mature fruit containing A. alboscutellatus. Peromyscus leucopus climbs L. alternifolia plants and removes fruit; M. pennsylvanicus cuts through the base of the plant, cuts the felled plant into small segments, and then consumes selected fruit. Both rodents have the potential to function as important predators of both L. alternifolia fruit and A. alboscutellatus during periods when the rodents are experiencing population flushes. Asynchronous flowering within individual L. alternifolia plants results in a wide range of both fruit and A. alboscutellatus developmental stages being present at the time plants are felled by M. pennsylvanicus. Because immature fruit do not complete development and larvae within them die when plants are felled (pers. obs.), M. pennsylvanicus can exert strong predation pressure on both L. alternifolia and A. alboscutellatus during population flushes.

During the winter months, white-throated sparrows, Zonotrichia albicollis, infre-

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entrance scars (white circular discs at top of fruit), $20 \times$; 9, overwintering cocoons of *A. alboscutellatus*, $25 \times$; 10, adult beetle trapped in the apical pore of an indehiscent *L. alternifolia* fruit, the pore shows signs of abrasion and chewing by the beetle, $60 \times$; 11, female *Pyemotes tritici* (white spheres in cocoon) and their victim, $25 \times$.

quently open L. alternifolia fruit and consume both beetles and wasps. Whitetail deer, Odocoileus virginianus, browse on L. alternifolia during the early summer months. Deer consume leaves, fruit, and some developing A. alboscutellatus larvae. In areas of high deer density, browsing dramatically reduces the number of fruit that plants produce and hence influences subsequent A. alboscutellatus population size. Once fruit begin to lignify during the late summer deer no longer browse on this plant.

Whereas A. alboscutellatus is subject to predation and parasitism within L. alternifolia fruit, predation on adult A. alboscutellatus following emergence from overwintering sites appears to be negligible. Despite extensive field observations, only twice has the author observed predation on adult beetles. In both instances, beetles visiting L. alternifolia flowers were captured by crab spiders, Misumena sp. (Araneida: Thomisidae).

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